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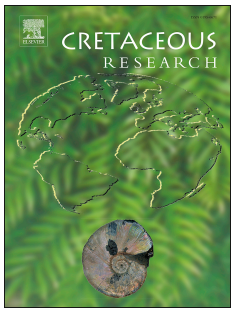

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- *Maichnus wetkaroae* igen. isp. nov. is a new trace fossil from the Albian of Patagonia
- It is the first trace fossil attributable to Odonata recorded from paleosols
- It is one of the oldest insect trace fossils recorded from paleosols
- It provides the first and unique evidence of ancestral burrowing behavior of petalurids
- This evidence supports some previous theoretical evolutionary scenarios for Odonata

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Jorge F. Genise: Conceptualization, Supervision, Investigation, Funding Acquisition, Writing - Original Draft, Writing-Review & Editing. **M. Victoria Sánchez:** Investigation, Methodology, Writing - Original Draft, Writing-Review & Editing. **Daniel G. Poiré:** Investigation, Funding Acquisition, Writing - Original Draft. **Mirta G. González:** Investigation, Writing-Original Draft.

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A fossorial petalurid trace fossil from the Albian of Patagonia

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ABSTRACT

Maichnus wetkaroae igen. isp. nov., from the Albian of Patagonia, is composed of two or three ellipsoidal oblate chambers connected to shafts that show swellings and concentrically laminated linings. Such laminated linings are also present in chambers, and probably originated by radial backfilling and/or the successive discharges of liquid organic excretions. This unique morphology occurs in paleosols showing evidence of waterlogging. Trace fossil morphology and the occurrence of traces in clusters in waterlogged soils indicate that *M. wetkaroae* igen. isp. nov. represents larval burrows of fossorial petalurids. This is the first record of Odonatan trace fossils from paleosols and also the oldest one. *M. wetkaroae* igen. isp. nov. is one of the oldest insect trace

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fossils recorded from paleosols. It represents the first and unique paleontological evidence of the ancient origin of the burrowing behavior of petalurids postulated only theoretically until now in evolutionary scenarios of Odonata.

Keywords: fossorial petalurid; trace fossil; *Maichnus wetkaroae* igen. isp. nov.*;* Albian; Patagonia

1. Introduction

The Cretaceous is a critical period for insect diversification and thus, paleoichnology clearly reflects this event. The oldest trace fossils in paleosols that unequivocally can be attributed to insects come from Cretaceous deposits of different regions. This fact responds to the appearance or diversification of key groups, such as bees, scarabs, termites and ants, but also cicadas and sphinx moths (Genise, 2016; Genise et al., 2020). Despite more than 30 years of intensive research on insect trace fossils in paleosols, the Cretaceous examples are few, in comparison with that of Cenozoic deposits (Genise, 2016). Thus, any insect trace fossil in paleosols that can be added to the Cretaceous record is a significant advance, a jewel. In addition, the trace fossil described herein from a paleosol is the first described for the order Odonata, also it reflects an uncommon habit for this group that is the fossoriality, and it contributes to the evolutionary history of the group.

The objectives of this contribution are: (1) To describe a new insect trace fossil in paleosols from the Albian of Patagonia, (2) To demonstrate that this trace fossil can

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be attributed to fossorial petalurids (Odonata), and (3) To contribute to the present knowledge of the evolutionary history of these living-fossil dragonflies.

2. Geologic setting

The Austral Basin, also known as Magallanes Basin, is located in the south-western margin of the South American plate. It comprises an area of approximately 230.000 km^2 over the southernmost extreme of Argentina and Chile. The Piedra Clavada Formation (= Kachaike Formation) (Feruglio in Fossa Mancini et al., 1938; Leanza, 1970) is a significant lithostratigraphic unit (306 m thick) from the Cretaceous sedimentary record of the Austral Basin in southern Patagonia, Argentina. It represents the final part of a rift stage, forming a large passive-margin delta system before the developing of a foreland basin stage (Biddle et al., 1986; Varela et al., 2008). The Piedra Clavada Formation is composed of fossiliferous yellowish sandstones interbedded with dark mudstones and heterolithic facies, and some conglomerates and coquina beds (Poiré and Franzese, 2010). These strata are interpreted as shallow marine to tidal-dominated delta deposits that change upward to estuarine coastal deposits, after a marked omission surface (Arbe 1989; Marinelli, 1998; Passalía et al., 2018; Poiré et al., 2002, 2017). This unit bears one of the most diverse marine, littoral and continental faunas and floras of the region (Archangelsky et al., 2008; Ballent et al., 2011; Passalía et al., 2018; Poiré et al., 2002, 2017). The age of the Piedra Clavada Formation had been estimated as late Aptian–Cenomanian according to its fossil content. Recently, Poiré et al. (2017) dated U-Pb zircons from two volcanic ash beds of

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68 the upper part of the Piedra Clavada Formation, obtaining concordance ages of 101.6 ±
69 0.9 My (29 zircons) and 99 ± 2.8 My (6 zircons), confirming a latest Albian age for the
70 top of the unit.

71 The trace fossils described here come from this upper section of the Piedra
72 Clavada Formation exposed at locality Puesto El Galpón (PG2: 49°29' 35.9'' S, 71°25'
73 18.2'' W), near Tres Lagos, Santa Cruz province, Argentina (Fig. 1A, B). Specimens occur
74 in a greyish fine tuff 30–35 cm thick extending about 300 m laterally, whereas the
75 trace fossils are restricted to two spots located 10 meters apart (Fig. 2A). The exposed
76 surface of this bed is whitish. The bed shows some remains of lamination in the upper
77 part, and also it shows some vertical cracks delimiting in some cases prismatic
78 structures, probably produced by weathering of the exposed surface (Fig. 2B). There
79 are no defined peds or macromorphological pedogenic characters other than small
80 rhizoliths (Fig. 2C). This bed is sandwiched between grey mudstones interpreted as
81 continental-estuarine deposits, bearing remains of plants, freshwater fishes and
82 turtles, and coquina beds with freshwater mollusks (Poiré et al., 2002, 2017) (Fig. 1B).

83 The paleosol bearing the trace fossils shows apedal soil material with a
84 predominantly massive microstructure. The porosity, which represents 5% of the total
85 sample, consists of channel and planar pores, which are poorly interconnected. The
86 voids, showing mostly rough walls, are irregular, elongated to round, and are not
87 orientated (Fig. 3A). Many voids present infillings of microcrystalline silica (Fig. 3B),
88 whereas others show calcite crystals (Fig. 3C). The coatings of Fe and Mn, constituting
89 hydromorphic features, are common (Fig. 3A, C). The coarse fraction, which represents
90 10% of the total sample, is mainly composed of quartz and feldspar crystals ranging in

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size from 10 μ to 20 μ (fine silt). The fine fraction, which represents 85% of the sample, is yellowish-brown and it is mainly composed of clay to very fine silt showing weak speckled to striated b-fabric. The recognized pedofeatures are brown, speckled with randomly distributed little nodules and coatings of Fe/Mn, and Mn dendrites (Fig. 3D), which indicate an immature and hydromorphic paleosol. The presence of calcite crystals suggests some degree of desiccation during the development of the soil.

3. Ichnotaxonomy

Maichnus igen. nov. *urn:lsid:zoobank.org:act:6E046C5E-90EE-42A5-A039-8339C95AF9E9*

Diagnosis: mostly sub-vertical, but also sub-horizontal burrow, straight or curved, which in some cases increases its diameter with depth and ends in one or two chambers. In the most complete specimens the shafts are divided into a proximal and a distal part. The proximal part shows a sharp contact between the shaft and the matrix and in some cases concentric layers, appearing as rings in cross section, surrounding the shaft. The infill is similar to the rock matrix and the cross section of the shaft is sub-circular to elliptical. The distal part, which may be sinuous, shows an irregular contact with the matrix and swellings of different sizes and shapes that in some cases resemble short chambers or branches. The infill of the chambers is similar to the rock matrix. The distal part may be connected to one ellipsoid, oblate, terminal chamber. In some cases, there is a second deeper chamber connected to the first one.

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The shaft is connected in few cases to one side of the chamber, or to the roof, either at the center or in most cases displaced to one extreme. Some chambers may show also concentric layers inside, which seen from top or bottom look like concentric rings.

Comments: There is no other ichnogenus comparable to *Maichnus* igen. nov..

Macanopsis, being a burrow with a terminal enlargement may resemble the simplest specimens of *Maichnus* igen. nov. However, either *Macanopsis*, or the known Krausichnidae, lack concentric layers in the wall. In contrast, concentric laminated burrows of asterosomids (i.e. *Cylindrichum*, *Rosselia* and *Asterosoma*) lack chambers. Somewhat different morphologies are grouped under the same ichnotaxon because it is possible to recognize a degree of intermediate morphologies among them that link the whole sample. In addition they co-occur only in two restricted spots of this outcrop.

Etymology: from the aboriginal *Aonikenk* language *ma* meaning cave or burrow and from the Greek *Ichnos* meaning trace.

Type ichnospecies: Maichnus wetkaroae isp. nov.

Maichnus wetkaroae isp nov. *urn:lsid:zoobank.org:act:3A935D1E-16E9-4129-96E5-24º07088BB5C*

(Figs.2, 4, 5)

Diagnosis: Only known ichnospecies, same as for the ichnogenus.

Etymology: From the aboriginal *Aonikenk* language *wetkaro* meaning dragonfly.

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136 *Holotype:* Specimen MPM-PIC 21587 from the Albian Piedra Clavada Formation
137 exposed at Puesto El Galpon, locality 2, Bed 20. It is deposited in the ichnological
138 collection of the Museo Padre Molina (MPM-PIC) from Rio Gallegos, Santa Cruz
139 province, Argentina.
140 *Paratypes:* Specimens MPM-PIC 21586, 21607, and 21634, from the same provenance
141 of the holotype.
142 *Examined material:* Other specimens collected and studied are MPM-PIC 21588–
143 21606, 21608–21633, 21635–21645 from the same provenance as the types. All
144 specimens are deposited in the ichnological collection of the Museo Padre Molina
145 (MPM-PIC), from Rio Gallegos, Santa Cruz province, Argentina.
146 *Description:* Specimens show different degrees of preservation and variations in their
147 morphology, but in most cases only part of the complete structure of the trace was
148 observable. The morphology described in the diagnosis is a reconstruction of the most
149 complete architecture and only the holotype (MPM-PIC 21587), preserving two
150 chambers and also the concentric layers in one of them, resembles this complete
151 morphology. Collected or just photographed pieces of burrows are sub-horizontal (n=
152 8) to sub-vertical (n=26), straight particularly in the proximal part (n= 4), or winding
153 particularly in the distal part (n=11). Other specimens, which show no distinction
154 between distal and proximal parts, are curved or sinuous (Fig. 2H). Total length of
155 shafts ranges from 8.5 mm, probably in the case of broken ones, to 93.6 mm (n=41).
156 Cross sections are sub-circular to elliptical and proximal parts are smaller in diameter
157 than distal parts (MPM-PIC 21634) (Fig. 2I). In the proximal part, diameters range from
158 3.4–6.5 mm to 12.5–14.5 mm (n=9). Concentric rings around the proximal parts, 0.7–

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159 3.4 mm wide, range in number from 1 to 5 (MPM-PIC 21618) (Fig. 2D). Longitudinal,
160 broken sections of the proximal shafts show that rings extend longitudinally forming a
161 thick lining (MPM-PIC 21586) (Fig. 4A) composed of concentric layers (Fig. 5A, C). The
162 infill of the proximal parts having concentric rings is similar to the rock matrix to the
163 naked eye, but in thin sections it displays stipple-speckled b-fabric. In cross section, at
164 the center it shows a pore (720 µ), which is partially filled with porous clay surrounding
165 a core of microcrystalline silica (MPM-PIC 21632) (Fig. 5B). There are six dark (oxidized)
166 lines radiating from the center of the pore, which is also surrounded by a somewhat
167 darkened layer 1 mm thick. About 4 mm from this layer, there are three oxidized rings,
168 each one also composed of concentric thin lines. The last ring at the boundary
169 between the trace and the paleosol is the best defined one (Fig. 5C). The rings may
170 show discontinuities or stepping patterns compatible with longitudinal microfaults
171 (Fig. 5D). Longitudinal thin sections show that rings are superposed cylinders, each one
172 delimited by an oxidized layer composed of two external darker lines, 25 µ thick, and
173 one lighter central one 50 µ thick (Fig. 5A).

174 In the distal part the swellings are 5.3–16.7 mm high (n=15), and their cross
175 sections are 3.4–17.3 mm (n=21). Swellings are in most cases connected to each other
176 by constrictions and those in the upper part are smaller than those in the deeper part
177 (MPM-PIC 21612) (Fig. 4B). In some cases the swellings are more likely short side
178 chambers (MPM-PIC 21634–35) (Fig. 2I, Fig. 4C). In some specimens the terminal
179 chamber is connected to a shaft in which swellings are more blurred (MPM-PIC 21610)
180 (Fig. 4D).

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Chambers are ellipsoid oblate and they are preserved as empty spaces or casts. The long axes range from 10.6 mm to 31.4 mm (n=30) and the short ones from 7 mm to 39.8 mm (n=33) (Fig. 2E-I). The height ranges from 4.2 mm to 23.8 mm (n=31). Chambers are preserved at the end of shafts, or in most cases isolated showing remains of shafts in the roof and in the floor (MPM-PIC 21588) (Fig. 4E). The shaft is connected in few cases to one side of the chamber (MPM-PIC 21607) (Fig. 2F, G), or to the roof, either at its center or in most cases displaced to one extreme. Some chambers show in the floor a single shaft that is connected to other chamber (MPM-PIC 21607)(Fig. 2F), or that is partly preserved with no observable end (MPM-PIC 21609) (Fig. 4F), or that is reduced to a scar (MPM-PIC 21609, 21591) (Fig. 4E). In a case, two chambers are connected by a constriction or very short shaft between them (MPM-PIC 21606) (Fig. 4G). Some chambers may show overlapping layers (1–4), which seen from top or bottom look like concentric rings in the best preserved specimens (MPM-PIC 21586–87, 21606, 21610) (Fig. 2E, 4H, I).

4. Discussion

Most insect trace fossils in paleosols are nests or chambers that originally contained air-breathing larvae with provisions, pupae or adults. Usually larvae die and provisions rot under water saturated conditions. Consequently insect traces are constructed in, and are indicative of, well aerated soils (Genise, 2016). The records of insect trace fossils in waterlogged soils have been unusual and dubious until now

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(Bellosi et al., 2013; Genise, 2016). *M. wetkaroae* igen. isp. nov. is the first for South America in such paleosols. Nests and chambers are complex structures that provide clear diagnostic characters for attributing trace fossils to insects. It is highly possible that insects have inhabited soils since the appearance of this substrate on Earth, but even so, trace fossils that can be unequivocally attributed to insects are known only from the Cretaceous onwards. The possibility to recognize older traces as made by insects is hampered by the lack of diagnostic characters in the morphologically simple traces. For instance, *Skolithos* can be produced by a lot of invertebrates in soils, lakes, and the sea. The recognition of insect traces in saturated soils may pose a similar problem. Nests and pupation chambers of air-breathing insects would be not expectable, or at least exceptional, in those soils (Genise, 2016).

In this sense, the water-breathing larvae of some species of petalurids (Odonata) belonging to the genera *Petalura, Tanypteryx and Uropetala* are exceptional for the following reasons. Firstly, they inhabit soft peaty soils in mires, seepages, bogs, swamps or along stream margins (Baird, 2012, 2014, 2017; Baird and Burgin, 2016; Benson and Baird, 2012; Davies, 1998; Svilha, 1959; Tillyard, 1911; Wolfe, 1935). Secondly, despite of their occurrence in saturated substrates, burrows show structural integrity and the possibility of recognizing their morphology (Baird, 2014, 2017; Wolfe, 1935). Thirdly, despite of the fact that their traces are relatively simple, they show well defined diagnostic characters (Baird, 2014 and references therein) to distinguish them from those produced by other organisms (Fig. 6).

Several characters shown by petalurid terrestrial habits and burrows match what is described herein for *Maichnus wetkaroae* igen. isp. nov.. They are found in

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226 waterlogged, soft, soils of different types of mires, swamps, bogs, fens, and seepages,
227 where their burrows always end below the water table (Baird, 2014, 2017; Benson and
228 Baird, 2012). The micromorphology of the paleosol where *M. wetkaroae* igen. isp. nov.
229 was found shows hydromorphic characters. One of the type of soils where *Petalura*
230 *gigantea* excavates their burrows is dense clay loams (Baird, 2014), showing a high
231 concentration of clays as the paleosol where *M. wetkaroae* igen. isp. nov. occurs. The
232 trace fossils were found clustered in two definite spots along an outcrop extending
233 laterally for about 300 m (Fig. 2A). The clustering of burrows was reported in *Petalura*
234 *gigantea, P. litorea* and *Uropetala carovei*. In *Petalura gigantea* and *P. litorea* the
235 clustering responds to the spatially aggregated ovipositing behavior of females. Larval
236 exuviae after emergence are found in clusters in potential contiguous breeding areas.
237 These aggregations result from different ovipositions of a single female, which are
238 accomplished in soil fissures, or among moss below the water level (Baird, 2014, 2017;
239 Baird and Burgin, 2013; Benson and Baird, 2012). The same is true for *Uropetala*
240 *carovei* (Winstanley and Rowe, 2012; Wolfe, 1953).

241 The clustering of burrows reflects single ovipositions. However, these clusters
242 may be inhabited by larvae of more than one stage since the duration of the larval
243 period may show great differences (Baird and Burgin, 2013; Tillyard, 1911; Wolfe,
244 1953). Diameters of burrows, which are enlarged along the larval life, depend on the
245 instar inhabiting them (Baird, 2014; Watson, 1965; Wolfe, 1953). In accordance,
246 burrows of different sizes can be found in the breeding spots, as is the case of *M.*
247 *wetkaroae* igen. isp. nov., showing diameters ranging from 3.5 mm to 14.5 mm.
248 Burrows are kept cleaned and empty by the larvae, which use the mask as a shovel to

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249 remove detritus from them (Wolfe, 1953). In contrast, Taketo (1971) claimed that *T.*
250 *pryeri* does not use the mask as a shovel to excavate, but the legs. Larvae of Odonata,
251 like *P. gigantea,* breathe by taking water through the anal opening and then expelling
252 it with great force through the anus too, which may cause the displacement of
253 sediment.

254 The last and most important comparison involves burrow morphology.
255 Petalurids show different types of burrows. The most complex ones of *P. gigantea*,
256 involving a boxwork of interconnected shafts and tunnels with multiple surface
257 openings, and occupied by several larvae described by Tillyard (1911), was then
258 disputed by Baird (2014). The latter author, based on his own observations of this
259 species, and the architecture of other species of this family, explained that probably
260 these systems were independent burrows excavated in close proximity to each other.
261 Similarly, U-shaped burrows, described by Wolfe (1953) for *U. carovei* are interpreted
262 as occasional connections of individual burrows of two different larvae, one of which
263 killed the other, and continued its development in the interconnected burrows (Baird,
264 2014). Simple burrows described, in *Tanypteryx hageni*, are composed of a vertical
265 proximal part, which may show a “pool” on the soil surface, and a distal sub-horizontal
266 part (Svihla, 1959; Taketo, 1971) (Fig. 6D). This type is similar to specimen MPM-PIC
267 21601 described herein (Fig. 2H). Other simplest burrows, excavated by young
268 nymphs, range from pits to vertical to sub-vertical short shafts in *Tanypteryx pryeri*
269 (Taketo, 1971, fig. 3a-d). Taketo (1971, Fig. 7H) also illustrates a horizontal burrow
270 running parallel to the soil surface. Horizontal burrows were also observed in the

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paleosol bearing *M. wetkaroae* igen. isp. nov. However, only in the case of MPM-PIC 21587 a horizontal channel possibly connected with the specimen was observed.

The typical petalurid burrow, represented by those of *P. gigantea* studied by Baird (2014) is composed of a sub-vertical shaft showing a number of side sub-horizontal chambers of different length and a terminal horizontal chamber. Terminal chambers are aligned either to one side of the shaft or centered. Shafts may show also swellings and small side chambers, smaller than the usual ones that correspond to the larval size (Fig. 6A, B). The side chambers may increase in size with increasing burrow depth in *P. hesperia* (Watson, 1965) and *U. carovei* (Wolfe, 1953) (Fig. 6C). In *P. gigantea*, the location of side chambers is probably controlled by different water table levels and burrows may have more than one terminal chamber in response to changes in water table level (Baird, 2014). Chambers would be useful for resting in groundwater and to increase the opportunities for ambush predation (Baird, 2014; Benson and Baird, 2012). *M. wetkaroae* igen. isp. nov. displays several of these characters such as (1) one or more terminal, tiered, chambers either aligned to one side or centered (Figs. 2F, 4G, 6A, B), and/or (2) small swellings in shafts that may increase in size with burrow depth becoming side chambers (Figs. 2I, 6C), and/or (3) simple shafts showing terminal enlargements (Figs. 2G, H, 4D, 6B, D).

As far as the preservation of these burrows in a very unstable substrate, there is some evidence of dehydration in the soil given by the presence of carbonate in thin sections (Fig. 3C). The desiccation of the substrate may contribute to the preservation of the traces. Davies (1998) mentioned that *P. gigantea* and *P. hesperia* excavate their

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burrows (breeding area) in soft boggy substrates that become brick-hard ones in the dry season.

The presence of concentric laminated layers in the burrows, which in cross sections appear as concentric rings, requires a particular analysis to elucidate the behaviour or process that may produce them. There are several hypotheses to be considered. Concentric laminated linings may be produced passively in burrows showing constricted apertures (Goldring, 1996). *M. wetkaroae* igen. isp. nov. lacks constricted apertures. However, constrictions at the entrances of burrows of *Petalura gigantea* and *P. litorea* were reported for by Tillyard (1911) and Baird et al. (2014, 2017). The possibility of the concentric layers being originated passively is then minimal, but cannot be discarded. Other possibility to consider is rhizoliths or paleorhizospheres, which frequently show concentric layers produced by the physical-chemical action of roots (Genise et al., 2011). In such cases the concentric layers surround the whole trace and are not located only at some places like in *M. wetkaroae* igen. isp.nov.. Also, the presence of chambers would not be expectable in root traces. Among those hypotheses involving invertebrates a passive/active origin of these structures may be posed. Concentric “fairy” rings are formed around gas domes (e.g. Noffke, 2010, figs III.22, IV.17) and also they may be present in the collapse of conical structures (Buck and Goldring, 2003, fig. 7B), which result from soft sediment flow inside a cavity or burrow, by the upward escape of gas, fluid or an organism, by vertical penetration of an organism or by dewatering. A simple experiment was carried out to simulate gas domes producing escaping bubbles by blowing through a cannula submerged in a soapy substrate contained in a beaker. The substrate was composed of

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316 pulverized rock from the original bed bearing *M. wetkaroae* igen. isp. nov., added with
317 around 21–26% of water. The excess or lack of water beyond this range results in no
318 rings. Rings are evinced by the alternation of greyish and yellowish bands (Fig. 7). Each
319 ring is actually an amount of substrate that is expelled with each bubble and deposited
320 as a ring around the ejection point. The bubbles produce similar “fairy rings” on the
321 surface that gas domes. However, such structures were not present along the pathway
322 of the bubble. So, such process can be discarded as an origin for *M. wetkaroae* igen.
323 isp. nov. concentric rings.

324 There are several active behaviors that may result in concentric layers, some of
325 them known from the asterosomids (Belaústegui and Gibert, 2013; Nara, 1995;
326 Seilacher, 2007). In *Cylindrichnus* the concentric layers suggest long-term habitation of
327 the burrow and the successive addition of mucous-impregnated pellets including
328 material introduced in the burrow from the surface (Belaústegui and Gibert, 2013). In
329 the case of *M. wetkaroae* igen. isp. nov. the thin sections show that there is no
330 addition of allochthonous substrate material, but oxidized layers which may
331 correspond to successive organic secretions. The differential impregnation with
332 organic matter causes a differential consolidation of layers that result in protruding
333 rings in weathered cross sections (Figs. 2 and 4). This type of multilaminated linings
334 resulting from successive discharges of liquid excretions are produced by sphinx moth
335 larvae and preserved in *Teisseirei* (Genise et al., 2013). Also it is conceivable that
336 concentric layers result from radial backfilling with the same material of the sediment
337 while burrowing (Seilacher, 2007). This behavior involving the compaction of new
338 material against the wall of the burrow, produce externally thinner rings and

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339 longitudinal cracks and microfaults parallel to the burrow axis (Belaústegui and Gibert,
340 2013; Nara, 1995; Seilacher, 2007). Microfaults are present in thin sections of *M.*
341 *wetkaroae* igen. isp. nov. (Fig. 5D) and the outer rings are usually thinner than the
342 internal ones (Fig. 2D). The presence of these features, compatible with radial
343 backfilling suggest that probably this behavior is mostly involved in the production of
344 this trace fossil, may be in combination with other ones, such as discharges of some
345 liquid excretions. Descriptions of petalurid burrows, which mostly came from unstable
346 substrates, lack details that can contribute to the further evaluation of the concentric
347 layers of *M. wetkaroae* igen. isp. nov.

348 How does *Maichnus wetkaroae* igen. isp. nov. contribute to the knowledge of
349 the evolutionary history of petalurids? According to a recent molecular phylogeny,
350 Petaluridae is a relict monophyletic group, which originated in Pangaea during the
351 Middle Jurassic (157.4 Ma), whereas the separation between the Laurasian and
352 Gondwanan clades took place 146.5 Ma and most speciation events for the extant
353 groups occurred before 70 Ma (Ware et al., 2014). The stem group, Petalurida, is also
354 placed in the Jurassic (Nel et al., 1998; Ware et al., 2014). The ages of 101.6 ± 0.9 Ma
355 and 99 ± 2.8 Ma for the interval where *M. wetkaroae* igen. isp. nov. occurs perfectly
356 match with the results of these phylogenies. It also records the presence of a
357 burrowing petalurid for the Albian of Patagonia, about 30 Ma prior to the speciation of
358 *Phenes raptor*, the non-burrowing single petalurid from South America. The non-
359 burrowing habit of this species is considered a derived trait in Petaluridae (Ware et al.,
360 2014), in which case *M. wetkaroae* igen. isp. nov. would be representing the behavior
361 of an ancestry of *P. raptor*. Baird (2019) considered that the burrowing behavior of the

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362 fossorial petalurids would have an origin predating the break-up of Pangaea. However,
363 there was no evidence of such behavior until now and the record of fossil larvae is
364 scarce (Nel et al., 1998). *M. wetkaroae* igen. isp. nov. records the burrowing behavior
365 of petalurids at least from the Albian of Patagonia. Fitzgerald and Barrett (1986)
366 proposed that some *Skolithos* from the Permian of Antarctica could be larval burrows
367 of dragonflies, and such proposal was considered by Ware et al. (2014) to support the
368 origin of petalurids in Antarctica during the Permian. However *Skolithos*, which can be
369 attributed to many organisms from marine, lacustrine and terrestrial environments,
370 lack any diagnostic characters comparable to petalurid burrows.

371 The Petaluridae have been already recorded from the Cretaceous of South
372 America (Nel et al., 1998) and particularly from Patagonia (Petrulevičius and Nel,
373 2003). The oldest Petaluridae known, *Argentinopetala archangelskyi*, comes from the
374 Aptian Anfiteatro de Ticó Formation (120 Ma) in Estancia Bajo Grande (Petrulevičius
375 and Nel, 2003), about 270 km northeastern from the locality of *M. wetkaroae* igen. isp.
376 nov.. It is represented by an almost complete wing, whose length was estimated to be
377 70 mm and accordingly its possible wingspan would be 14.5 cm. Burrows of the last
378 instar larvae of *U. carovei*, whose adults have a wingspan of 13 cm, range from 2.8 cm
379 to 3.1 cm (Wolfe, 1953) whereas those of *T. hageni,* with a wingspan of 8.5 cm, range
380 from 0.9 cm to 1.75 cm (Svihla, 1959). The last instar larvae of *P. gigantea*, whose
381 adults have a wingspan of 11–12 cm, produce burrows up to 4.5 cm in diameter (Baird,
382 2014). The maximum burrow diameter recorded for *M. wetkaroae* igen. isp. nov. is
383 1.45 cm. If these burrows correspond to last instar larvae, then the size of adults would
384 be comparable to those of *T. hageni*. Other recorded diameters for younger larvae of

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385 extant species are 1.75 cm for *P. gigantea* (Tillyard, 1911) and 1 mm for the second
386 instar larvae of *U. carovei* (Wolfe, 1953). The extant Patagonian petalurid, *Phenes*
387 *raptor*, whose larvae are not fossorial, has a wingspan of 15 cm (Muzón, 2009). In
388 sum, the diameter of *M. wetkaroae* igen. isp. nov. is compatible with those of burrows
389 of the extant smaller petalurids. The Aptian Patagonian *Argentinopetala archangelskyi,*
390 and the extant *P. raptor*, would be a larger species than the Albian trace maker of *M.*
391 *wetkaroae* igen. isp. nov.
392
393 **5. Conclusions**
394
395 The Albian *Maichnus wetkaroae* igen. isp. nov. is a new insect trace fossil from
396 waterlogged paleosols that shows a unique morphology which is different from
397 previously described ones. The most complete preserved architecture of the trace
398 fossil shows two or more ellipsoidal to ovoid chambers connected by a shaft with
399 swellings. Both shafts and chambers show concentric layers, which probably originated
400 by the radial backfilling and/or the successive discharges of liquid organic excretions.
401 Also the occurrence of this trace fossil in saturated soils is unusual, since most of the
402 other insect trace fossils occur in well drained soils. The presence in saturated soils,
403 occurrence in clusters, and burrow morphology indicate that *M. wetkaroae* igen. isp.
404 nov. represents larval burrows of fossorial petalurids (Odonata). *M. wetkaroae* igen.
405 isp. nov. would be the first trace recorded from paleosols for the entire Order, and also
406 one of the oldest insect trace fossils recovered from paleosols. The Albian record of a
407 burrowing petalurid trace fossil matches with the proposed phylogeny for the group,

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and it is placed 30 Ma before the speciation of *Phenes raptor*, the derived non-burrowing single extant petalurid from South America. *M. wetkaroae* igen. isp. nov., from the Albian of Patagonia, represents the first and unique evidence of the ancient origin of the burrowing behavior of petalurids postulated theoretically in evolutionary scenarios.

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Figure captions

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562 **Fig.1.** Location map and stratigraphic log. (**A**) Location map. The arrow indicates the
563 locality of Puesto El Galpon 2 (PG2), (**B**) Stratigraphic log of PG2. P: mudstone, H:
564 heterolithic, A: sandstone, C: conglomerate.

565

566 **Fig. 2.** *Maichnus wetkaroae* igen. isp. nov. in outcrops. (**A**) Arrows indicate the
567 stratigraphic level and the two sites where *M. wetkaroae* igen. isp. nov. occurs,
568 (**B**) Trace fossil bearing paleosol showing remains of lamination on top. Scale bar: 10
569 cm, (**C**) Tiny ferrugineous rhizoliths. Scale bar: 1 cm, (**D**) Cross section of the proximal
570 part of a shaft showing concentric rings (MPM-PIC 21618). Scale bar: 1
571 cm, (**E**) Holotype (MPM-PIC 21587) composed of a shaft ending in a chamber showing
572 concentric layers. In the box is the bottom of the chamber showing the rings. Scale
573 bars: 1 cm, (**F**) Paratype (MPM-PIC 21607) showing from top to bottom, a shaft (1), a
574 first chamber (2), a connection thin shaft (3) and a terminal chamber with infill (4),
575 below this another chamber (5). Scale bar: 1 cm, (**G**) Specimen (MPM-PIC 21591)
576 showing the distal part of a shaft ending in a chamber (arrow). Scale bar: 1
577 cm, (**H**) Specimen (MPM-PIC 21601) composed of a simple inclined and curved burrow
578 ending in an enlargement. Scale bar: 1 cm, (**I**) Paratype (MPM-PIC 21634) showing a
579 proximal part on top followed by a distal part with swellings and short side chambers
580 (arrows). Scale bar: 1 cm.

581

582 **Fig. 3.** Paleosol micromorphology. (**A**) Irregular, elongated to round, non-orientated
583 voids. Scale bar: 1 mm, (**B**) Voids showing infills of microcrystalline silica. Scale bar:

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584 100 µ, (**C**) Voids filled with Fe/Mn and calcite crystals. Scale bar: 100 µ, (**D**) Manganese
585 dendrites. Scale bar: 500 µ.
586
587 **Fig. 4.** *Maichnus wetkaroae* igen. isp. nov. (**A**) Paratype (MPM-PIC 21586) showing a
588 thick lining around the shaft, (**B**) Specimen (MPM-PIC 21612) showing swellings in the
589 distal part of the shaft, (**C**) Specimen (MPM-PIC 21635) showing a short side chamber
590 (arrow), (**D**) Specimen (MPM-PIC 21610) where swellings may be not so evident at the
591 distal part of the shaft, (**E**) Specimen (MPM-PIC 21588) showing a short remain of shaft
592 connected at the roof of a chamber (arrow) and a scar at the floor (arrow), (**F**)
593 Specimen (MPM-PIC 21609) showing remains of a shaft at the floor of a chamber
594 (arrow), (**G**) Specimen (MPM-PIC 21606) composed of two chambers connected by a
595 very short shaft, (**H**) The same specimen in (**G**) showing the floor of the lower chamber
596 and the concentric layers at one end (arrow), (**I**) Chamber from specimen illustrated in
597 (**D**) showing concentric rings on top. All scale bars: 1 cm.
598
599 **Fig.5.** Micromorphology of *Maichnus wetkaroae* igen. isp. nov. (**A**) Longitudinal section
600 of a specimen (MPM-PIC 21630) showing superposed layers, each one delimited by
601 oxidized lines. Scale bar: 200 µ, (**B**) Cross section of a specimen (MPM-PIC 21632)
602 showing a central pore partially filled with clay surrounding a core of microcrystalline
603 silica. Note the oxidized radiating lines. Scale bar: 500 µ, (**C**) Cross section of a
604 specimen (MPM-PIC 21632) in the matrix showing the oxidized concentric rings. Scale
605 bar: 2 mm, (**D**) Detail of (**C**) showing a step and a microfault in the rings (arrow).Scale
606 bar: 200 µ.

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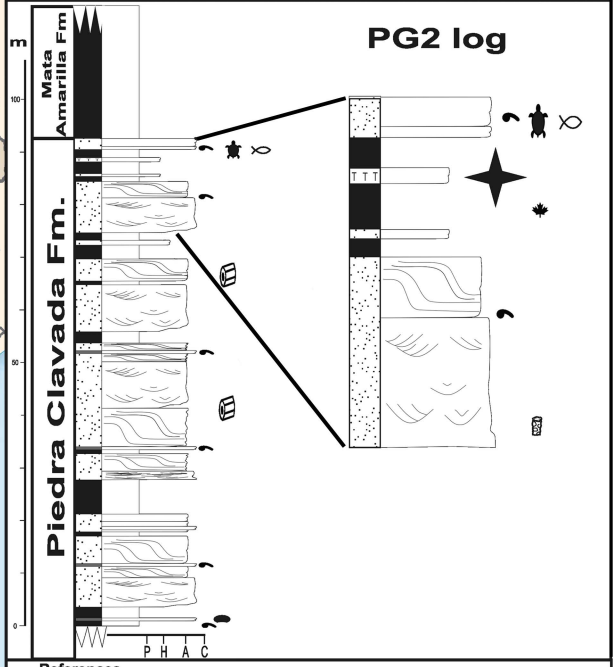
608 **Fig. 6.** Burrows of extant petalurids redrawn from Wolfe (1953), Taketo (1971), and
609 Baird (2014). (**A**) and (**B**) Burrows of *Petalurea gigantea* showing tiered horizontal
610 chambers. Compare with specimen MPM-PIC 21607 illustrated in Fig. 2F, (**C**) Burrow of
611 *Uropetala carovei* showing inclined side chambers. The pattern is similar to *Petalura*
612 *hesperia*. Compare with MPM-PIC 21634 illustrated in Fig. 2I, (**D**) Burrow of *Tanypteryx*
613 *pryeri* showing a simple pattern composed of a curved burrow that enlarges towards
614 the end. Compare with specimen MPM-PIC 21601 illustrated in Fig. 2H, (**E**) Burrow of
615 *Petalurea gigantea* showing a sinuous morphology similar to the holotype of *M.*
616 *wetkaroae* igen. isp nov. illustrated in Fig. 2E.

617

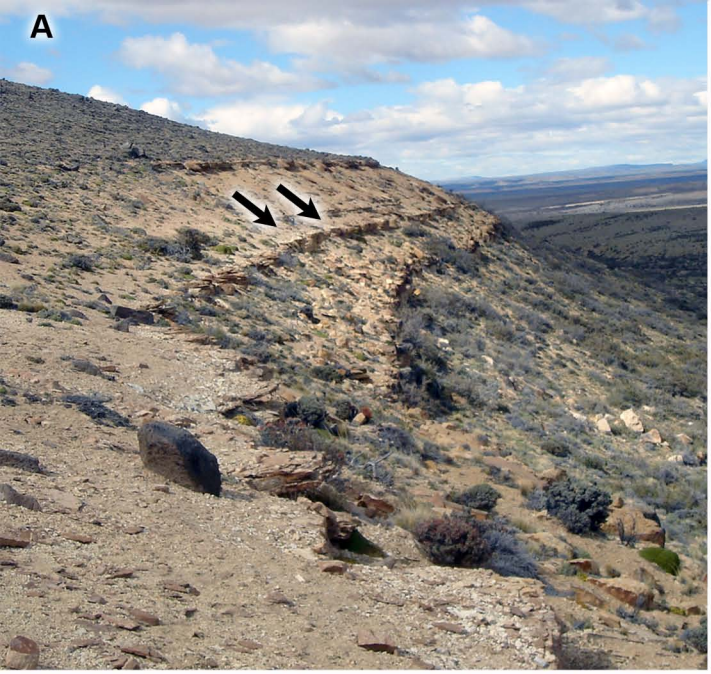
618 **Fig. 7.** Concentric rings produced experimentally by escaping bubbles. (**A**) and (**B**)
619 Arrows point to the insertion hole of the cannula submerged in the substrate that
620 produced the bubbles by blowing. The central depression/hole was left by the
621 escaping bubbles. The red color in (**B**) marks the limit between the surface of the
622 substrate (red) and the dome (greyish with two rings red coloured). Rings are evinced
623 by the alternation of greyish and yellowish bands. Each ring is actually an amount of
624 substrate that is expelled with each bubble and deposited as a ring around the ejection
625 point.

626



References

- Bioclastic conglomerate sandstones
- Sandstones
- Heterolithic beds
- Mudstones
- Massive
- Mud clasts
- Horizontal lamination
- Planar cross-bedding
- Sigmoidal cross-bedding
- Diffuse sigmoidal cross-bedding
- Trough cross-bedding
- Diffuse trough cross-bedding
- Ripple marks
- Bioclasts
- Leaves
- Transported trunks
- Ostracods
- Turtles
- Fish scales
- *Ophiomorpha* isp.
- *Maichnus wetkaroae*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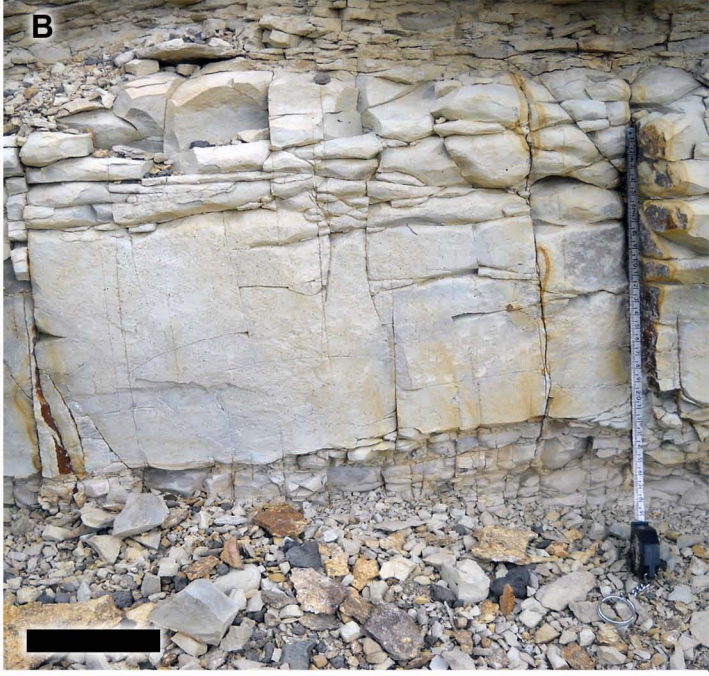
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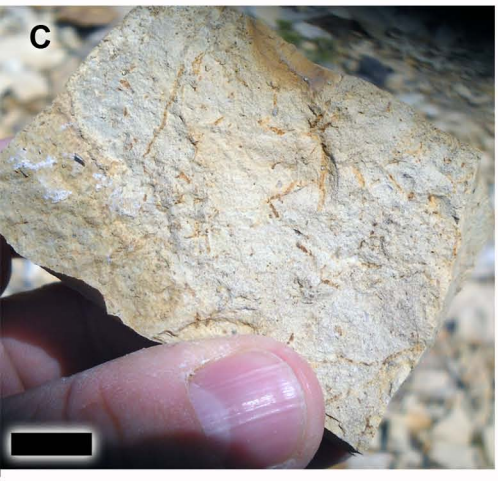
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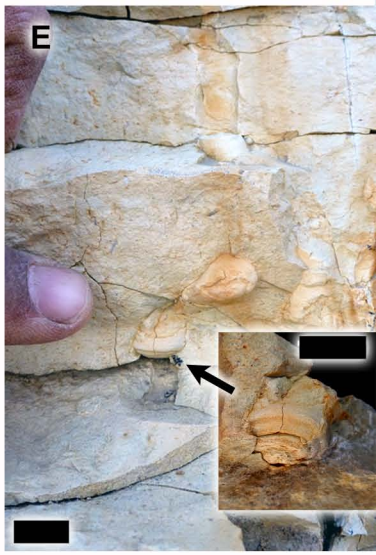
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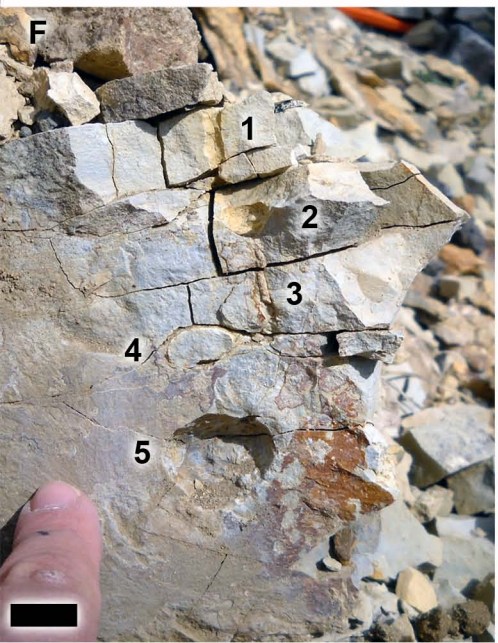
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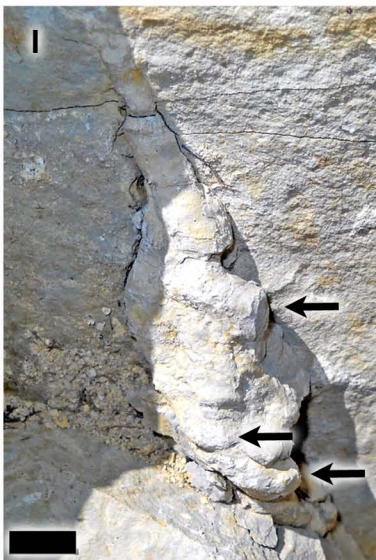
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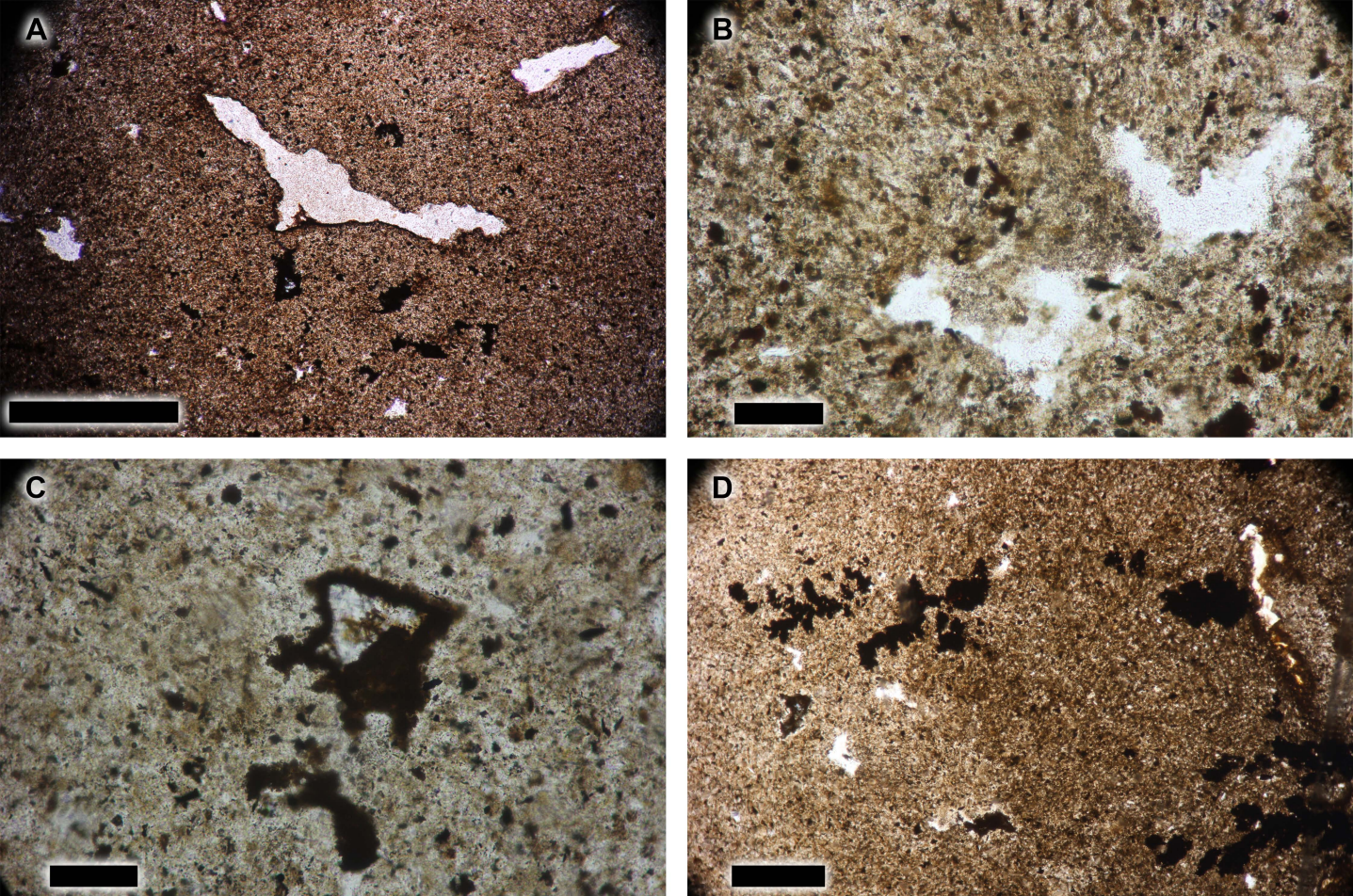
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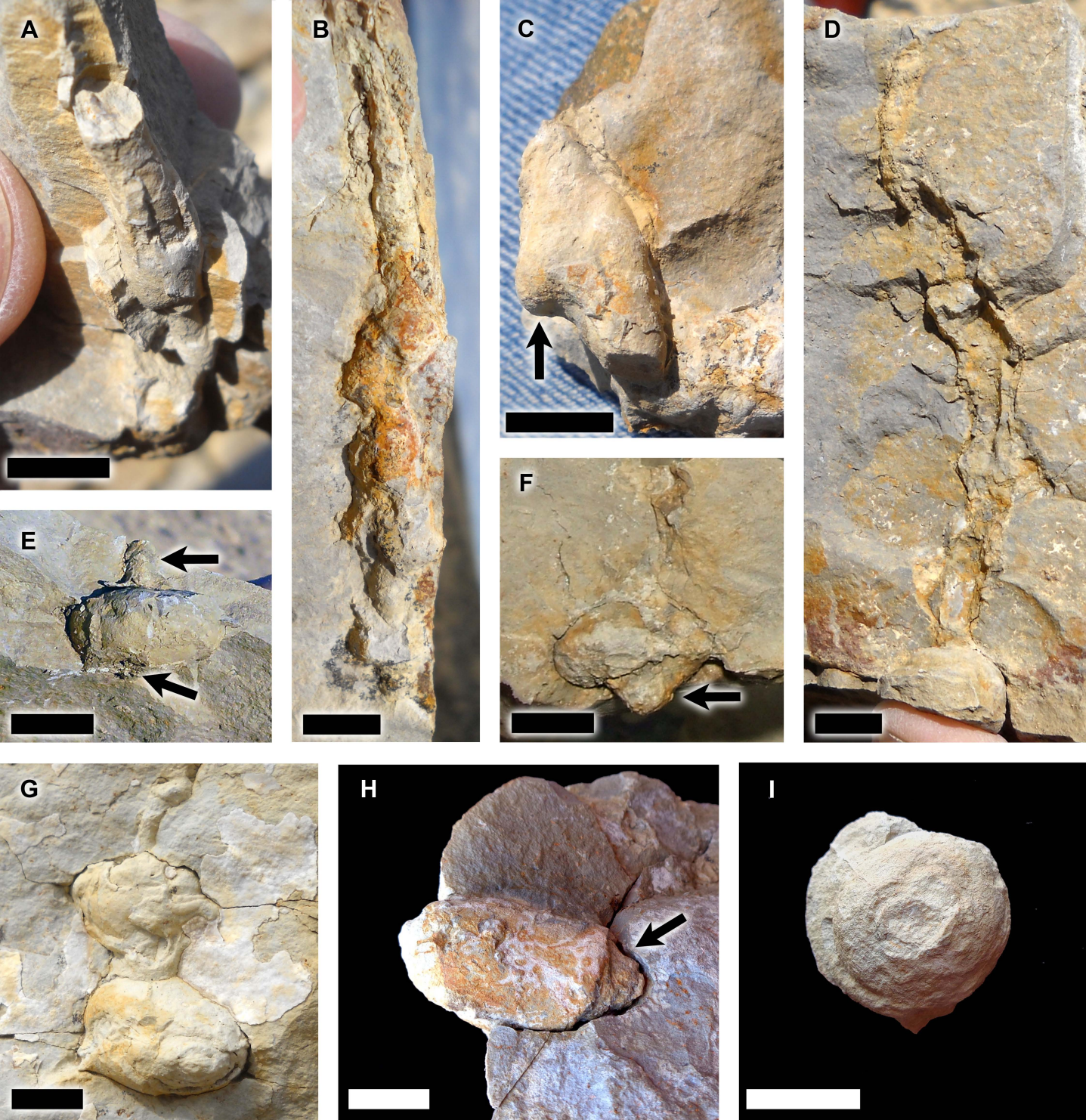
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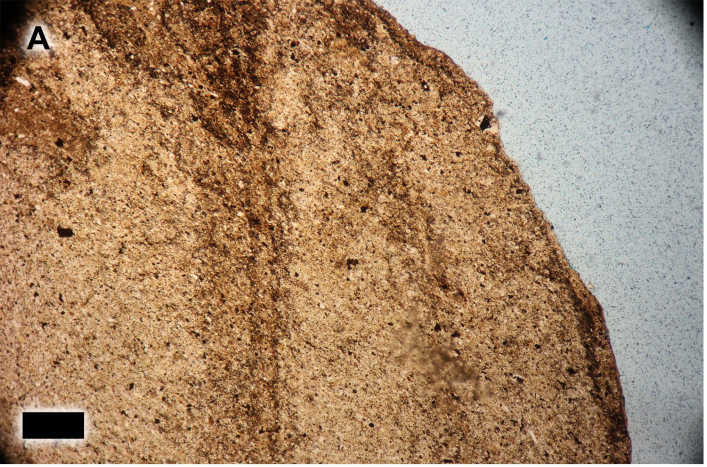
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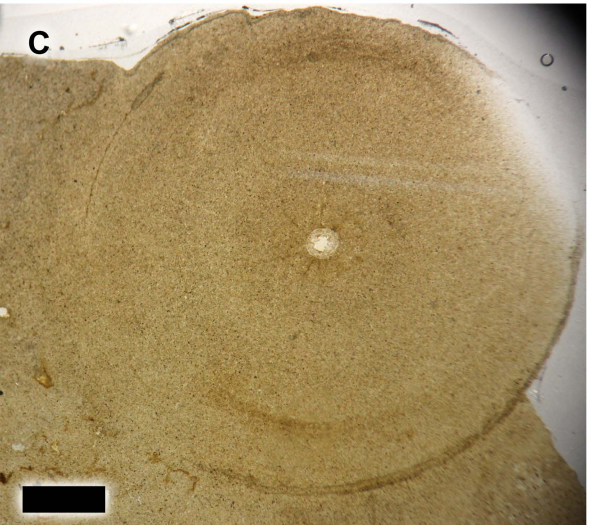
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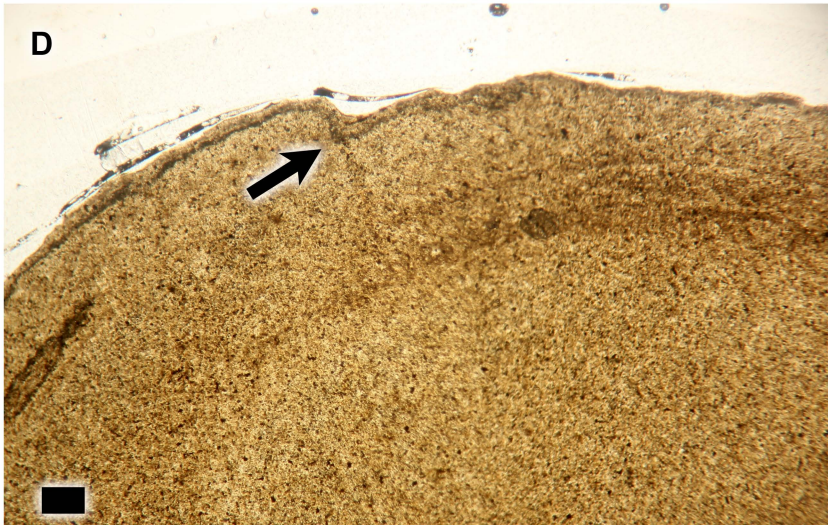
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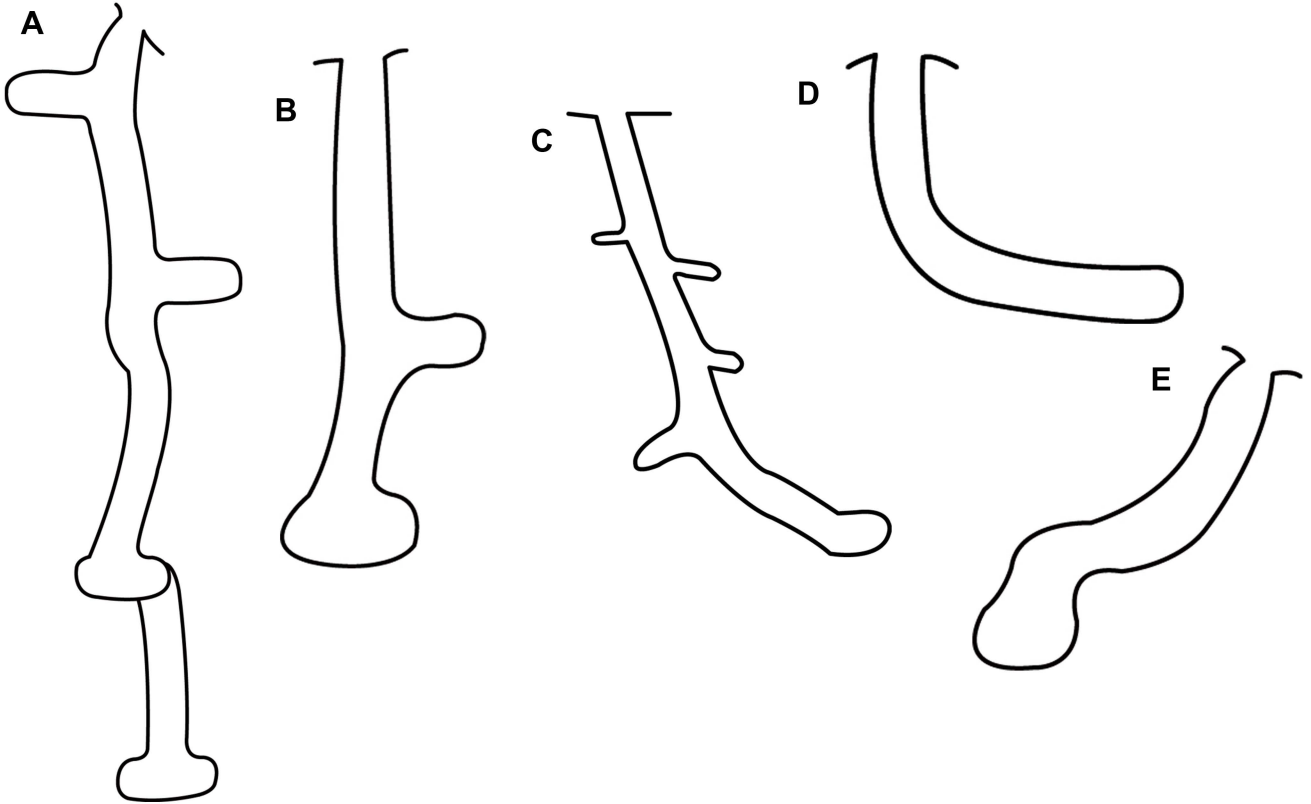
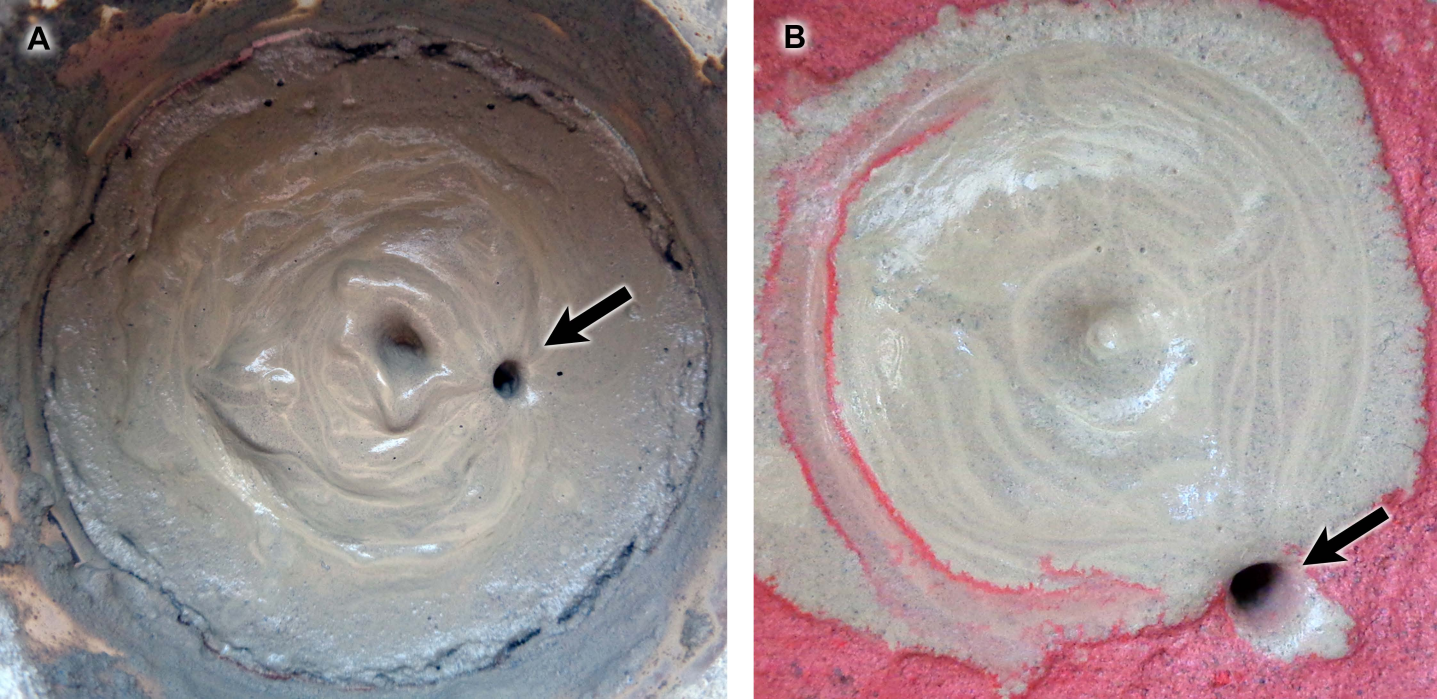

A
B
C
D
E


A
B

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- *Maichnus wetkaroae* igen. isp. nov. is a new trace fossil from the Albian of Patagonia
- It is the first trace fossil attributable to Odonata recorded from paleosols
- It is one of the oldest insect trace fossils recorded from paleosols
- It provides the first and unique evidence of ancestral burrowing behavior of petalurids
- This evidence supports some previous theoretical evolutionary scenarios for Odonata

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Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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